THE OCCURRENCE OF BISPORANGIATE STROBILI IN SUBALPINE BLACK SPRUCE

W. H. WEIDLICH[1] AND J. A. TEERI[2]

Successful growth and sexual reproduction in subalpine black spruce (*Picea mariana* (Mill.) BSP.) in New Hampshire are limited by exposure and the low mean temperature of the warmest month of the growing season, as in the northern parts of the species range (Teeri, 1968). At timberline the frequency of individuals successfully reproducing by seed is much less than in the forests at lower elevations. In Krummholz patches above the timberline, which in the White Mountains of New Hampshire occurs between 4500-4700 ft., reproduction appears to be accomplished primarily by vegetative layering of the prostrate stems, with only sporadic occurrence of female strobili (Teeri, 1969). At the upper elevational limit of female strobilus production (ca. 4,800 feet above sea level), bisporangiate strobili occasionally occur on prostrate plants of black spruce.

Bisporangiate strobili have been reported for many genera of conifers (Chamberlain, 1935) including spruce (Santamour, 1959), and information on the morphological distribution of sexes is present in the literature (Chamberlain, 1935; Richter, 1932; Zobel, 1952; Santamour, 1959; Black, 1961; and Elis, 1970). This paper describes the anatomy of bisporangiate strobili of subalpine black spruce and correlates their occurrence with changing environmental conditions along an elevational gradient on Mt. Washington, New Hampshire.

METHODS

The study area was on an east-facing slope of Mt. Washington, New Hampshire. It included at its lower elevation (2,800 ft.) a well-developed red spruce (*Picea rubens*)-

[1]Harvard University Cabot Foundation, Petersham, Mass. 01366.
[2]Department of Biology, University of Chicago, Chicago, Ill. 60637.

balsam fir (*Abies balsamea*) forest. Occasional black spruce colonies were present in this forest in sites subjected to cold air drainage or on wind exposed ridge crests. At the upper elevation (5,000 ft.) the study area was within the alpine zone in which prostrate Krummholz colonies of black spruce were scattered on the tundra. Maximum-minimum recording thermometers were placed in ventilated wood shelters at two elevations in the study area and were read weekly for the 1967 growing season. The shelters were located in the foliage of black spruce plants at each station. Additional temperature data were obtained from records of the weather observatory at the summit of the mountain.

Bisporangiate strobili of *Picea mariana* were fixed in FAA in the field. The fixed strobili were dehydrated in tertiary butyl alcohol, embedded in Paraplast, and sectioned at 10-12 μ on a rotary microtome. The sections were stained with safranin and fast green.

RESULTS

The mean weekly temperatures for the three stations of the transect are illustrated in Figure 1. The right-hand axis indicates the sexual reproductive status of black spruce along the transect. At lower and middle elevations (2,800-4,600 ft.) normal male and female strobili are produced. At about 4,300 feet the size and frequency of female strobili decrease. Along with the decrease in size, the strobili become increasingly deformed. The 10°C isotherm for the warmest month of the year is approximately the upper elevational limit for successful sexual reproduction of black spruce in the White Mountains of New Hampshire (Teeri, 1968). None of the female strobili above 5,000 feet was observed to release seed; in fact they usually decomposed during the growing season. Upon dissection of these cones, ¾ of the seeds were hollow or grossly deformed (Teeri, 1968).

Bisporangiate strobili occur occasionally at the elevation where female strobili start to disappear. They are borne

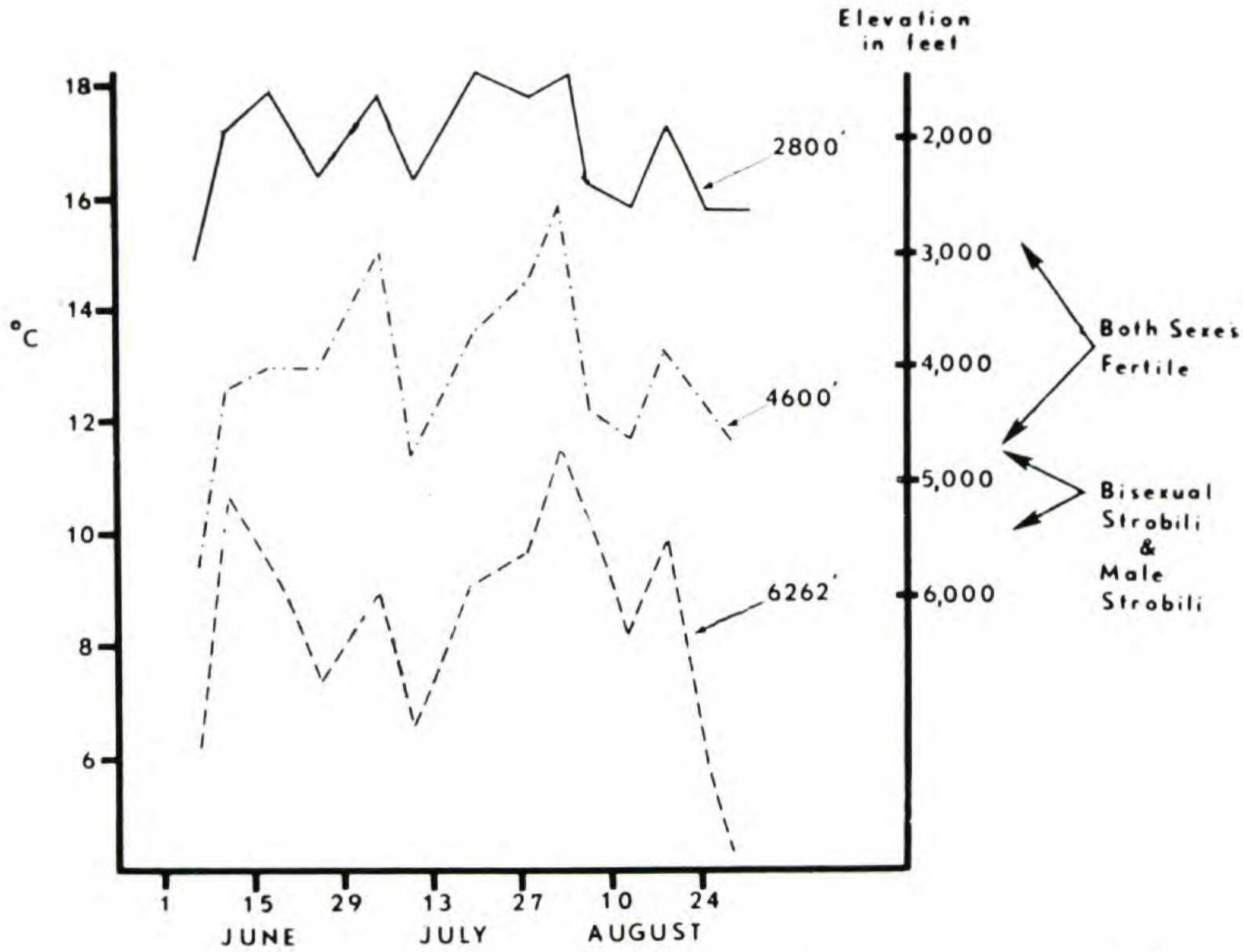

Fig. 1. Interrelations of cumulative mean air temperature at 3 elevations and fertility of subalpine black spruce. At higher elevations the bisporangiate strobili produce a small amount of fertile pollen but no viable seeds. At the same elevation male strobili produce fertile pollen, but the female strobili all appear stunted and sterile.

just below the terminal portion of new shoots (the normal position for female strobili) and are bisporangiate in one of two arrangements. In the first arrangement (longitudinally bisporangiate), the distal half of the strobilus bears ovuliferous scales, and the proximal half microsporangia (Fig. 2 A). In the second arrangement (laterally bisporangiate) the two sexes are distributed in a bilateral arrangement along the axis of the strobilus (Fig. 2 B).

The transition from male to female in the longitudinally bisporangiate strobilus is more gradual than in the laterally bisporangiate strobilus. The microsporangia in the laterally bisporangiate strobilus have already shed most of their pollen, and appear normal. The microsporophylls also seem normal (Fig. 2 B). The microsporophylls in the lower portion of the longitudinally bisporangiate strobilus

Fig. 2. Distribution of sexes in bisporangiate strobili of black spruce. A. Longitudinally bisporangiate strobilus (20×). B. Laterally bisporangiate strobilus (20×). (B) bract; (M) microsporangium; (MS) microsporophyll; (O) ovule; (OV) ovuliferous scale.

are regular in appearance and pollen in the microsporangia seems normally developed (Fig. 2 A). The ovuliferous scales in the laterally bisporangiate strobilus and the female portion of the longitudinally bisporangiate strobilus are regular in appearance. The ovules which they bear appear to be normal (no ovules are in the plane of section in Fig. 2 A) and are in the usual stage of development for conifers at pollination (Chamberlain, 1935; Foster and Gifford, 1959). Each ovule consists of a free cellular gametophyte, nucellus, and an integument that is reflexed at the micropyle to allow entry of pollen into the pollen chamber (Fig. 2 B).

Some unusual morphological characteristics are present in the transition zone between male and female portions of the longitudinally bisporangiate strobilus. The bracts subtending the ovuliferous scales in the lowermost portion of the female section often bear aborted microsporangia (B in Fig. 3 B). Bracts distal to the transition zone bear no microsporangia. Of less frequent occurrence in the transition zone are bracts that bear two microsporangia containing fully developed pollen (Fig. 3 A). The vascular tissue in the bract (or microsporophyll) exhibits the normal arrangement of xylem and phloem (phloem abaxial to the xylem), whereas the vascular tissue in the associated ovuliferous scale exhibits the typical reversal of xylem and phloem (phloem adaxial to the xylem) in the ovuliferous scale of conifers (Chamberlain, 1935; Foster and Gifford, 1959). The normal orientation of xylem and phloem indicates that the structure bearing microsporangia in Figure 3 A is a bract subtending an ovuliferous scale, and is also functioning as a microsporophyll. This unusual condition has also been reported for *Pinus* (Chamberlain. 1935).

DISCUSSION

Sexual reproduction is not common in subalpine black spruce in New England (Teeri, 1969). Reduced fertility is associated with a decrease in size of the female strobili

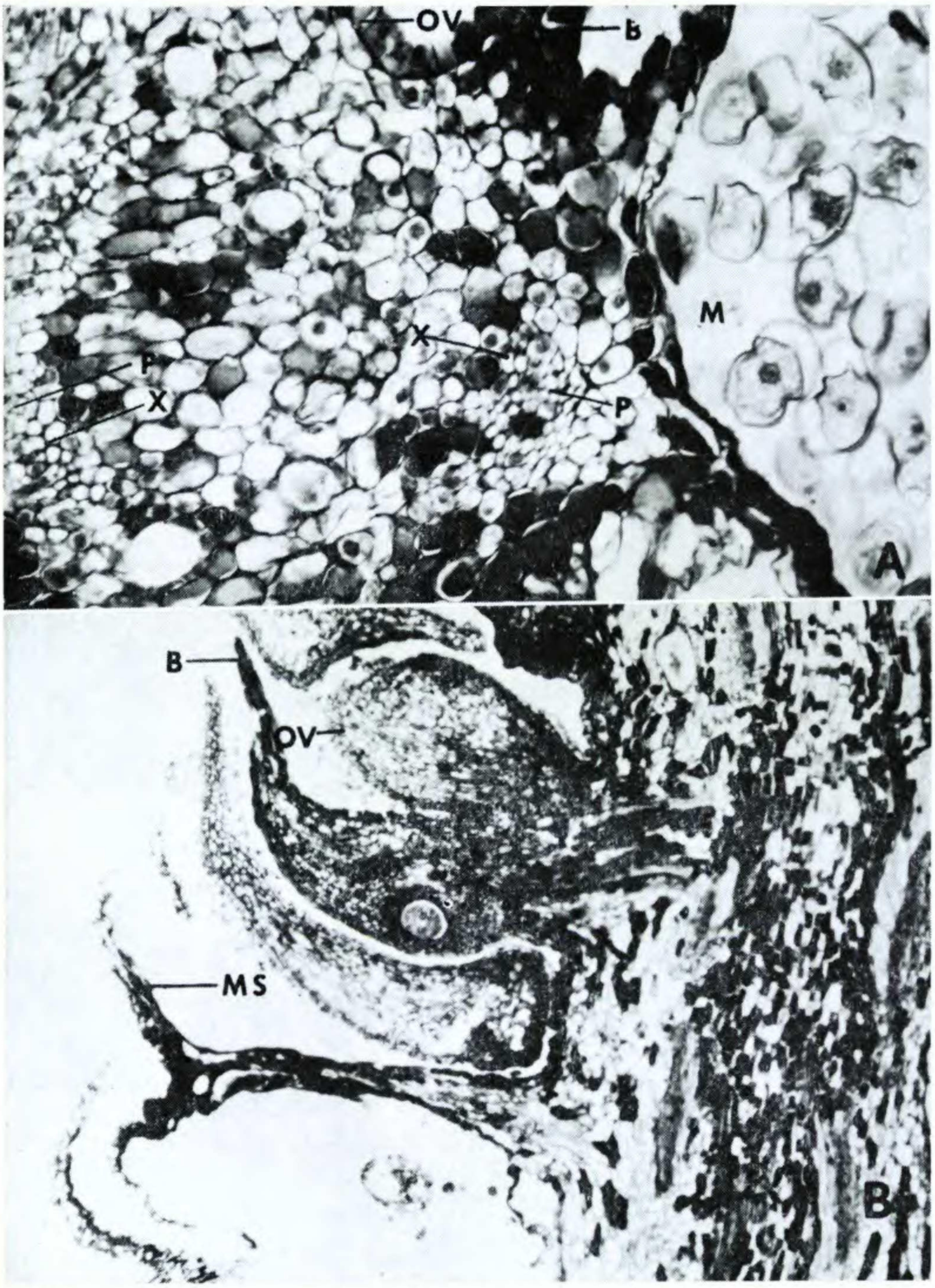

Fig. 3. A. Cross section of ovuliferous scale-bract complex with bract bearing a microsporangium containing pollen (170×). B. Longitudinal section of a bract bearing an aborted microsporangium (50×). (B) bract; (M) microsporangium; (MS) microsporophyll; (OV) ovuliferous scale; (P) phloem; (X) xylem.

and a decrease in the production of viable seed. As the elevation increases on Mt. Washington, the temperature and duration of the growing season decrease, and precipitation increases (Teeri, 1968). Thus, conditions favorable for sexual reproduction diminish with increasing elevation. The size and number of viable seeds per female strobilus decrease with increasing elevation up to timberline, whereas the male cones are affected principally above timberline. Therefore, the breakdown in sexual reproduction seems to specifically involve poor development of the female strobilus prior to pollination, and failure to produce viable seed following pollination since no viable seeds were found at high elevations.

In an extensive study on the reproduction of black spruce, Fraser (1957, 1966) determined that a heavy seed year follows a hot dry summer in the arctic and alpine ranges of the species. He found that a lack of warm dry weather prevents the build-up of reserve photosynthates necessary for a good seed crop and that more reproductive buds form during a good summer with a high carbohydrate accumulation. Thus the conditions prevailing at the time when buds are formed determine whether strobili or leaves will be produced from buds in reproductive positions along the branches. The decrease in optimum conditions for carbohydrate accumulation and strobili formation as elevation increases in the Presidential Range of New Hampshire may be responsible for a lack of reproductive bud inception and development at higher elevations.

In the genus *Abies* approximately the same number of reproductive buds is formed annually and hence inception is considered to be independent of external factors (Elis, 1970). The further development of these primordia is reported to be apparently influenced by external factors. For example, buds transitional between vegetative buds and female strobili were observed to occur in positions which would normally be occupied by buds of female strobili. These transitional buds produced either ovuliferous scales proximally and short needles distally, eventually developing into shoots, or they produced needles proximally and subsequently developed ovuliferous scales. One bisporangiate strobilus was observed that was female in the terminal portions and male at the base.

As in *Abies*, changes in external conditions may be responsible for the production of bisporangiate strobili in black spruce. The conditions under which a strobilus begins development may favor formation of microsporophylls, while later conditions may favor the production of ovuliferous scales. The laterally bisporangiate strobilus is difficult to fit into this general explanation. If the sexual expression of a reproductive bud is controlled by a sensitive physiological balance of growth regulating substances or nutrients, this balance could be upset in a longitudinal or lateral manner at the environmental limits of the species tolerance. In the case of the longitudinally bisporangiate strobilus, either the strobilus apical meristem or the embryonic primordia that were cut off by it changed their course of development completely; whereas in the case of the laterally bisporangiate strobilus, either the strobilus apical meristem or the primordia alternate between micro- and mega-physiological states during which male and female reproductive structures are formed.

Bisporangiate strobili and abnormal positioning of female strobili have been reported for *Pinus contorta* (Black, 1961) and balsam fir (Schooley, 1967). In these cases the female and bisporangiate strobili replace male strobili in the male clusters at the base of the new shoot. These female strobili are somewhat stunted and produce a smaller number of viable seeds than do normally positioned ones. It is apparent from these studies that the position of a reproductive bud does not have complete influence on its development. The bisporangiate strobili of black spruce are also borne in positions where female strobili normally occur, but this position does not absolutely predispose the strobilus to total female expression.

The larger female strobili probably require more photosynthate for development than male strobili (Fraser, 1957), and bisporangiate strobili occur where environmental conditions are marginal for female strobilus production. Environmental extremes have been invoked elsewhere as an explanation of the sporadic occurrence of bisporangiate strobili (Black, 1961; Santamour, 1959; Elis, 1970). There are several factors that could explain why the male strobili continue to form normally at elevations where female strobili fail to complete normal development. Fraser (1966) has observed that male cones of black spruce differentiate about a week earlier than female strobili. At the end of the relatively brief growing season at timberline, the earlier onset of development of male strobili would allow a longer period for initial development. In addition, the female strobili are considerably larger than the male strobili and in the growth-limiting timberline environment, the smaller male strobili are more likely to receive the necessary photosynthate for completion of development than the larger female strobili.

Chamberlain (1935) discusses the various morphological interpretations of the bract and ovuliferous scale. He considers the bract of the female strobilus to be homologous to the microsporophyll of the male cone. The bisporangiate strobili described in this paper are teratological phenomena and any phylogenetic inferences or interpretations of homology should be drawn with considerable caution. However, the fact that bracts subtending ovuliferous scales in the transition zone of the longitudinally bisporangiate strobilus bear microsporangia tends to substantiate Chamberlain's (1935) conclusion as to the nature of the bract in the female strobilus of conifers.

SUMMARY

Bisporangiate strobili are occasionally produced on plants of black spruce at timberline (4500-4700 ft.) in the mountains of New Hampshire. These abnormal strobili occur at the upper elevational limit of production of "normal" female strobili. The air temperatures of the growing season at this elevation are near the lower limit (mean July

temperature ca. 10°C) reported for successful growth and reproduction of black spruce in other parts of its range.

The bisporangiate strobili occupy positions on the terminal portions of the branches where female strobili would normally occur. At pollination the ovules and pollen grains appear normal. Bisporangiate strobili are probably indicative of changing or adverse environmental conditions causing changes in physiological states and subsequent morphogenesis and sex expression. Bracts subtending ovuliferous scales may bear microsporangia in the transition zone between sexes in longitudinally bisporangiate strobili.

ACKNOWLEDGMENTS

We thank Dr. C. G. Nast for encouragement during the course of this investigation and Dr. R. A. White for reviewing the manuscript. We also thank Ms. T. S. Teeri for first discovering bisporangiate cones on subalpine black spruce in the White Mountains of New Hampshire and drawing them to our attention.

LITERATURE CITED

BLACK, T. M. 1961. Abnormalities of the reproductive system of *Pinus contorta* Loudon. Ann. Bot. n.s. **25**: 21-28.

CHAMBERLAIN, C. J. 1935. Gymnosperms. Structure and Evolution. University of Chicago Press. 484 p.

ELIS, S. 1970. Reproduction and reproductive irregularities of *Abies lasiocarpa* and *A. grandis*. Can. Jour. Bot. **48**: 141-143.

FOSTER, A. S., & E. M. GIFFORD, JR. 1959. Comparative Morphology of Vascular Plants. W. H. Freeman and Co., San Francisco. 555 p.

FRASER, D. A. 1957. The relation of environmental factors to flowering in spruce. *In:* K. V. THIMANN, ED. The physiology of forest trees. The Ronald Press Co., N. Y. Chapter 34.

————. 1966. Vegetative and reproductive growth of Black Spruce (*Picea mariana* (Mill.) BSP.) at Chalk River, Ontario, Canada. Can. Jour. Bot. **44**: 567-580.

RICHTER, F. I. 1932. Bisexual flowers among the pines. Jour. For. **30**: 873.

SANTAMOUR, F. S. 1959. Bisexual conelets in Spruce. Morris Arbor. Bull. **10**: 10-11.

SCHOOLEY, H. O. 1967. Aberrant ovulate cones in Balsam Fir. For. Sci. **13**: 102-104.

TEERI, J. A. 1968. The ecology of subalpine Black Spruce in New England. Masters Thesis, University of New Hampshire. 62 p.

———. 1969. The phytogeography of subalpine Black Spruce in New England. Rhodora **71**: 1-6.

ZOBEL, B. J. 1952. Abnormal cone formation in pines. Texas Jour. Sci. **4**: 517-520.

DEPT. OF BOTANY AND PLANT PATHOLOGY
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, N.H. 03824